100 YEARS Journal of Ecology

British Ecological Society

Journal of Ecology 2012, **100**, 1216–1223 doi: 10.1111/j.1365-2745.2012.02004.x

Can floral traits predict an invasive plant's impact on native plant–pollinator communities?

Michelle R. Gibson[1], David M. Richardson[1] and Anton Pauw[2]*

[1]*Department of Botany & Zoology, Centre for Invasion Biology, Stellenbosch University, 7602, Matieland, South Africa; and* [2]*Department of Botany & Zoology, Stellenbosch University, 7602, Matieland, South Africa*

Summary

1. The possession of certain floral traits can determine which insects visit a plant species. If two species possess similar floral traits that determine shared flower visitors, floral traits can be said to mediate plant–plant interactions. Such indirect interactions are important for understanding fundamental relationships of plant communities, such as competition and facilitation but thus far have only been tested within a native community context.

2. We test whether floral-trait similarity can be used to predict interactions between an invasive plant and co-occurring native species in South Africa's Cape Floristic Region. We surveyed flower visitation at invaded and uninvaded plots across four sites and correlated floral-trait similarity between invasive and native species with both invasion impact on native flower visitation and flower visitor overlap of natives and the invasive species.

3. Similarity of all traits (categorical and continuous) and categorical traits alone explained invasion impact (flower visitor overlap) between the native and invasive species. The majority of flower visitor overlap was attributed to the native honeybee *Apis mellifera* subsp. *capensis*.

4. This study is the first to show that floral traits can be used to predict novel plant–plant interactions, even amongst ecologically generalized flower visitors and plants and to predict potential impacts of an invasive species on native flowering communities. However, floral traits were not useful for predicting changes in visitation to plant species.

5. *Synthesis.* Results advance our understanding of the role of plant traits in ecological communities and reveal that they are important in mediating not only plant–pollinator interactions but also plant–plant interactions. Our findings also shed light on invasive–native plant interactions via pollinators and have the potential to predict certain invasion impacts.

Key-words: *Acacia saligna*, biological invasions, flower morphology, fynbos, generalist, honeybee, invasion ecology, plant–insect interactions, plant–plant interactions, pollination syndromes

Introduction

Facilitation and competition are among the most important interactions that occur between neighbouring plant species (Connell & Slatyer 1977; Schlüter *et al.* 2009). Plants can compete with one another for abiotic resources such as shade and light or compete for or facilitate each other's soil nutrient uptake. Interactions may also be mediated by a third party such as flower-foraging insects. The way flowering plant species interact with pollinators, and hence the outcome of the interaction between plant species, is mediated and determined by floral traits, which are important in attracting flower visitors (Faegri and van der Pijl 1979).

*Correspondence author. E-mail: apauw@sun.ac.za

The theory of pollination syndromes posits that floral traits can be used to predict the identity of flower visitors (Vogel 1954; Faegri and van der Pijl 1979; Pauw 2006). Many pollination studies use floral traits to predict plant–pollinator interactions (e.g. Fenster *et al.* 2004, Lázaro, Hegland and Totland 2008), but there is very little evidence that floral traits can predict plant–plant interactions (Herrera *et al.* 2002; Hegland & Totland 2005; Danieli-Silva *et al.* 2011). Predicting the impact of one species on another species or on the surrounding community is one of the fundamental goals of invasion ecology (Elton 1958) as alien species can have irreversible effects on native ecosystems (Higgins *et al.* 1999; Evans *et al.* 2001; Traveset & Richardson 2006; 2011). Progress has been made in finding traits associated with invasiveness (Pyšek & Richardson 2007), such as growth rate, seed mass and resprouting ability (Gallagher *et al.* 2011; Gibson *et al.* 2011;

Lamarque, Delzon and Lortie 2011). However, much less progress has been made in finding correlates of impact (Williamson 2001). In the plant invasion literature, a meta-analysis suggests that alien plants with floral traits similar to native species may have a more detrimental impact on native species than those with dissimilar traits (Morales & Traveset 2009). Here, we test whether floral traits can predict plant–plant interactions in an invasion context. Elucidation of the drivers of impacts of introduced species is important because invasive plants can exert disproportionate impacts on pollination and reproductive success of native species (Bartomeus, Vila and Santamaria 2008b; Moroń *et al.* 2009). Knowledge of these drivers is critical for the long-term management of native plant communities.

Studies that use floral traits as predictors of plant–pollinator and plant–plant interactions have thus far only looked at native plant species (Hegland & Totland 2005; Lázaro, Hegland and Totland 2008). However, there is evidence that pollinator functional groups can be predicted in novel plant–animal interactions based on floral-trait similarity despite a lack of shared history of interactions (Geerts & Pauw 2009). Our aim was to determine whether floral traits can be used to predict the impact of an invasive plant, *Acacia saligna*, on native plant species. *Acacia saligna* is a major invader of fynbos vegetation in South Africa where it flowers simultaneously with many native species during spring, making it an ideal system for testing this prediction. Our study involved correlating the impact of invasion on visitation rate to native plant species with their floral similarity to *A. saligna*. We predict that plants with floral traits most similar to those of *A. saligna* are more likely to be impacted due to pollinator sharing. Such information is needed to advance our understanding of the full spectrum of effects that introduced species have in invaded ecosystems, including subtle effects that may have long-term consequences for ecosystem functioning (Pyšek & Richardson 2010).

Materials and methods

STUDY SITE

Study sites were located in sclerophyllous, fire-prone shrublands on sandy, nutrient-poor soil characteristic of the south-western coastal region of the Cape Floristic Region in South Africa's Western Cape province (Cowling, Richardson and Mustart 1997). Vegetation at three study sites is classified as Agulhas Limestone Fynbos and at the fourth as Atlantis Sand Fynbos (Mucina & Rutherford 2006). Agulhas Limestone Fynbos is characterized by low shrubs mixed with taller proteoid vegetation on low hills and plains. The families Asteraceae and Proteaceae are prominent, with species of Restionaceae assuming dominance in sandier patches. The area receives an average annual rainfall of 410–660 mm, and most rain falls between June and August. Mean summer and winter temperature extremes range from 25.5 to 7.0 °C, respectively. Atlantis Sand Fynbos grows on flat sand plains where Restionaceae and Proteaceae are dominant plant families with Asteraceae and patches of Ericaceae occurring in seepages. Peak precipitation occurs between May and August, mean annual precipitation is 290–660 mm and temperature extremes range from 27.9 °C (February) to 7 °C (July). Atlantis Sand Fynbos is listed as a vulnerable vegetation type, and 40% of its original extent has been transformed (Mucina & Rutherford 2006).

Acacia saligna is one of the most widespread and abundant woody invasive species in both vegetation types and is a major threat to biodiversity and ecosystem functioning in these ecosystems (Rebelo *et al.* 2006). This evergreen tree species, introduced from Australia in the mid 19th century, flowers from August through October in South Africa and is considered one of the most problematic invasive plant species in the region due to its ability to alter, dominate and replace native vegetation, thereby causing major changes to ecosystem functioning (Le Maitre *et al.* 2011). Its floral morphology is similar to that of most African and Australian acacias with yellow globular inflorescences composed of multiple individual flowers with easily accessible rewards, making it attractive and accessible to a wide range of potential flower visitors (Stone *et al.* 2003; Gibson *et al.* 2011).

SAMPLE DESIGN

We surveyed plant communities at four sites during 2009 (September–October) and 2010 (August–October). Sites were located at least 3 km apart. Each site comprised an invaded plot (*A. saligna* present) and an uninvaded plot (no *A. saligna*), with plots located between 0 and 700 m apart. Plots were located close together to ensure that native species composition and structure were similar between the invaded and uninvaded plots. To test whether number of floral displays, average area per floral display and floral unit density of focal species were approximately similar between all invaded and uninvaded plots and were unlikely to influence flower visitation patterns, we compared these variables using a paired Wilcoxon signed-rank test (number floral displays/plot, $V = 533$, $P = 0.314$; area/floral display (m^2), $V = 528$, $P = 0.910$; floral units/m^2, $V = 497$, $P = 0.823$). At each site, three focal native species were chosen (hereafter 'focal species') that comprised the most common and/or widespread flowering taxa in both invaded and uninvaded plots (Fig. 1). All field sites contained different focal species and, within a site, all species were from different families except at Mamre where two of the three species are in the family Asteraceae. All focal species were from different families from that of the invasive alien plant, *A. saligna* (Fabaceae).

FLOWER VISITOR OBSERVATIONS

Observations of flower visitors at invaded and uninvaded plots took place between 08:00 and 17:00 and were conducted simultaneously to ensure similar weather conditions. We observed a 1-m-radius patch of each focal species at three different areas separated by 60–100 m in the invaded and uninvaded plots to reduce the influence of local effects (e.g. floral and spatial autocorrelation effects). In the invaded area, we selected observation patches that were within 30–50 m of the nearest *A. saligna* stand. Observations lasted 15–30 min and each focal species was observed for a total of 90 min. During the observation, we recorded number of flowers observed, number of legitimate flower visits (where the visitor contacted the reproductive parts of the flower) and visitor identity. When visitors could not be identified in the field, we collected the insect for later identification.

FLORAL TRAITS

We measured categorical and continuous traits of all plant species at invaded and uninvaded plots that were shown to be important in predicting flower visitor identity or visitation rates in the previous studies (Table 1) (Hegland & Totland 2005; Lázaro, Hegland and Totland

Fig. 1. Plant species and families used to investigate the relationship between floral-trait similarity and impact of an invasive plant *(Acacia saligna*; k*)* on native flower–insect interactions. (a) *Chrysanthemoides monilifera* (Asteraceae); (b) *Roepera fulva* (Zygophyllaceae); (c) *Ursinia anthemoides* (Asteraceae); (d) *Mimetes cucullatus* (Proteaceae); (e) *Dimorphotheca pluvialis* (Asteraceae); (f) *Erica imbricata* (Ericaceae); (g) *Erica parviflora* (Ericaceae); (h) *Muraltia satureioides* (Polygalaceae); (i) *Leucospermum patersonii* (Proteaceae); (j) *Cyphia volubilis* (Campanuleaceae); (k) *Acacia saligna* (Fabaceae); (l) *Pelargonium betulinum* (Geraniaceae); (m) *Polycarena lilacina* (Scrophulariaceae) (photographs: M. R. Gibson).

2008; Morales & Traveset 2009). Floral traits were separated into two general categories following Hegland & Totland (2005). Categorical traits included clustering (S = solitary, I = inflorescence), colour (white, pink/purple, yellow, orange/pink), shape (O = open, C = closed) and symmetry (A = actinomorphic, Z = zygomorphic). Continuous traits included average number of floral displays, average area per floral display and floral unit density within a 30- to 50-m-radius area surrounding the observation area of each focal species. A floral display comprised a recognizable visual unit of conspecific flowers and referred to a single flower or group of flowers depending on the species (*sensu* Hegland & Totland 2005). Floral display area was measured as the size of the flowering plant patch using one of three formulas: πr^2 if circular and vertically flat; length × width if rectangular; or $\pi r^2 + 2\pi r^2$ if circular with a depth dimension. A floral unit is a single flower head, or part of a multiple head, from which a medium-sized bee has to fly rather than walk to reach another floral unit of the same species (Dicks, Corbet and Pywell 2002).

DATA ANALYSES

To test the relationship between floral-trait similarity of focal species with *A. saligna* and the effect of *A. saligna* on insect visitation to focal species, we used change in flower visitation to focal species between invaded and uninvaded plots and flower visitor overlap between the focal and invasive species as response variables and floral-trait similarity as the explanatory variable. We consider 'change in visitation' and 'flower visitor overlap' to be appropriate proxies for potential impact of *A. saligna* on the native community as visitation acts as an important precursor to pollen deposition and pollination (Alarcón 2009) and visitor overlap increases the chances of *A. saligna* pollen contamination of natives. Change in visitation between invaded and uninvaded plots was calculated using the relative neighbour effect index (RNE; Markham & Chanway 1996; Muñoz & Cavieres 2008), where RNE = $(V_{mixed} - V_{control})$/max $(V_{mixed,}\ V_{control})$ and V_{mixed} = flower visitation rate when *A. saligna* is present, $V_{control}$ = flower visitation rate when *A. saligna* is absent and max $(V_{mixed,}\ V_{control})$ = the maximum of the two values. Values range from −1 to 1, with −1 indicating total competition and 1 indicating total facilitation. Flower visitor overlap was calculated as the proportion of total visitation rate to a focal species that was comprised of visitor groups that also visited *A. saligna*, with values ranging from 0 to 1, and was calculated on both a family and morphospecies level. Floral-trait similarities were calculated for categorical traits alone, continuous traits alone, and for categorical and continuous traits combined using a dis-

Table 1. Plant species and floral traits in invaded plots used in analyses

Site	Plant species	Cluster	Colour	Shape	Symmetry	Average number of floral displays	Average area/ floral display (m^2)	Average number of floral units/ m^2	Primary overlapping visitor w/*Acacia saligna* (% total visitation rate to focal sp.)	Flower visitor overlap with *Acacia saligna*	
										Family level	Morphospecies level
Mamre	*Polycarena lilacina*	I	White	C	A	45.7	2.47	42.2	Coleoptera: Scraptiidae sp. (27)	0.70	0.38
	Ursinia anthemoides	I	Yellow	C	A	9.67	3870	17.9	Coleoptera: Scraptiidae sp. (31)	0.81	0.45
	Dimorphotheca pluvialis	I	White	C	A	36.0	23.2	10.7	Coleoptera: Scraptiidae sp. (28)	0.91	0.34
	*Acacia saligna**	I	Yellow	O	A	45.0	2790	50.0	–	–	–
Koude Vlakte 2009	*Chrysanthemoides monilifera*	I	Yellow	C	A	21.7	13.2	56.0	Coleoptera: Anthicidae sp. (11)	0.56	0.18
	Muraltia satureioides	S	Pink/ purple	C	Z	13.3	47.6	140	N/a	0.00	0.00
	Roepera fulva	I	Yellow	O	A	9.67	14.5	271	Hymenoptera: *Apis mellifera* subsp. *capensis* (80)	0.95	0.88
	*Acacia saligna**	I	Yellow	O	A	12.4	136	49.8	–	–	–
Witkrans	*Leucospermum patersonii*	I	Orange/ red	C	A	10.0	4.71	8.91	Hymenoptera: *Apis mellifera* subsp. *capensis* (34)	0.87	0.36
	Pelargonium betulinum	I	Pink/ purple	C	Z	16.7	1.96	12.6	Hymenoptera: *Apis mellifera* subsp. *capensis* (61)	0.61	0.61
	Erica parviflora	I	Pink/ purple	C	A	8.67	98.7	325	Hymenoptera: *Apis mellifera* subsp. *capensis* (39)	0.45	0.40
	*Acacia saligna**	I	Yellow	O	A	16.5	107	84.4	–	–	–
Koude Vlakte 2010	*Chrysanthemoides monilifera*	I	Yellow	C	A	12.3	35.5	63.4	Coleoptera: Mordellidae (13); Hymenoptera: Formicidae sp. (13)	0.60	0.28
	Muraltia satureioides	S	Pink/ purple	C	Z	5.00	124	167	Hymenoptera: Formicidae sp. (10)	0.10	0.10
	Roepera fulva	I	Yellow	O	A	9.00	1.62	229	Hymenoptera: *Apis mellifera* subsp. *capensis* (41)	0.83	0.44
	*Acacia saligna**	I	Yellow	O	A	11.3	170	93.2	–	–	–
Walschacres	*Erica imbricata*	I	Pink/ purple	C	A	70.3	10.2	135	Hymenoptera: *Apis mellifera* subsp. *capensis* (26)	0.61	0.26
	Cyphia volubilis	S	Pink/ purple	C	Z	26.0	0.03	181	Hymenoptera: *Apis mellifera* subsp. *capensis* (9)	0.48	0.09
	Mimetes cucullatus	I	Orange/ red	C	Z	38.7	5.18	4.11	N/a	0.00	0.00
	*Acacia saligna**	I	Yellow	O	A	1.00	1065	52.9	–	–	–

* indicates the invasive species.

I, inflorescence; S, solitary; C, closed; O, open; A, actinomorphic; Z, zygomorphic.

similarity matrix with the 'daisy' function and Gower's dissimilarity metric in the 'cluster' package (Maechler, M., Rousseeuw, P., Struyf, A. & Hubert, M. 2005, Unpublished data). We used Gower's similarity coefficient because it can be computed from qualitative and quantitative variables and is appropriate when descriptors (floral traits) are multistate and/or not dimensionally homogenous (Legendre & Legendre 1998).

We fitted a linear mixed-effects model using the 'lme' function in the 'nlme' package (Pinheiro *et al.* 2011) to measure the correlation between floral-trait similarity and RNE, and floral-trait similarity and flower visitor overlap. Linear mixed-effects models account for pseudoreplication resulting from the nesting of random effects (Crawley 2007). Site and year were specified as random effects with year nested within site to account for nonindependency of observations for plants occurring at the same site and of focal species surveyed in both years. We also tested the relationship between flower visitor overlap and RNE (Appendix S1) using linear mixed-effects models as a high flower visitor overlap between two flowering species may result in a change in visitation rate to one or both species.

To test which categorical traits were important in determining floral-trait similarity and flower visitor overlap between *A. saligna* and focal species, we used logistical regression with trait dissimilarity and flower visitor overlap as the response variables and individual trait scores as the explanatory variable. To do this, we used a generalized linear model (GLM) with binomial errors and corrected the standard errors for underdispersion using a quasi-GLM model with a dispersion parameter.

We used R for all statistical analysis (R Development Core Team 2011).

Results

We found that focal species with floral traits more similar to *A. saligna* shared more flower visitors with *A. saligna*. Such results support our initial prediction that species that are more florally similar to *A. saligna* are more likely to be impacted due to flower visitor sharing. Categorical trait similarity and similarity of categorical and continuous traits combined were significantly correlated with flower visitor overlap at the morphospecies level (categorical traits: coefficient = −0.466, standard error = 0.145, $t = -3.23$, $P = 0.0104$; categorical and continuous traits combined: coefficient = −0.757, standard error = 0.256, $t = -2.95$, $P = 0.0161$; Fig. 2d,e) and family level (categorical traits: coefficient = −0.715, standard error = 0.165, $t = -4.33$, $P = 0.0019$; categorical and continuous traits combined: coefficient = −1.22, standard error = 0.307, $t = -3.96$, $P = 0.0033$; Fig. 2a,b). Continuous traits alone had no influence on flower visitor overlap (morphospecies level: coefficient = 0.774, standard error = 0.814, $t = 0.0950$, $P = 0.367$; family level: coefficient = 0.537, standard error = 0.979, $t = 0.549$, $P = 0.596$; Fig. 2c,f). We found no significant relationship between the potential impact of invasion as measured by RNE and flower visitor overlap (morphospecies level: coefficient = −0.613, standard error = 0.366, $t = -1.67$, $P = 0.120$; family level: coefficient = −0.319, standard error = 0.288, $t = -1.11$, $P = 0.297$) or floral-trait similarity (categorical traits only: coefficient = 0.282, standard error = 0.273, $t = 1.03$, $P = 0.329$; continuous traits only: coefficient = 0.0408, standard error = 0.956, $t = 0.0427$, $P = 0.967$; categorical and continuous traits combined: coefficient = 0.453, standard error = 0.456, $t = 0.992$, $P = 0.347$; Fig. 3).

We found symmetry (zygomorphic; coefficient = 2.46, $t = 3.62$, $P = 0.00473$) and colour (yellow; coefficient = −2.25, $t = -2.42$, $P = 0.0339$) to be significantly

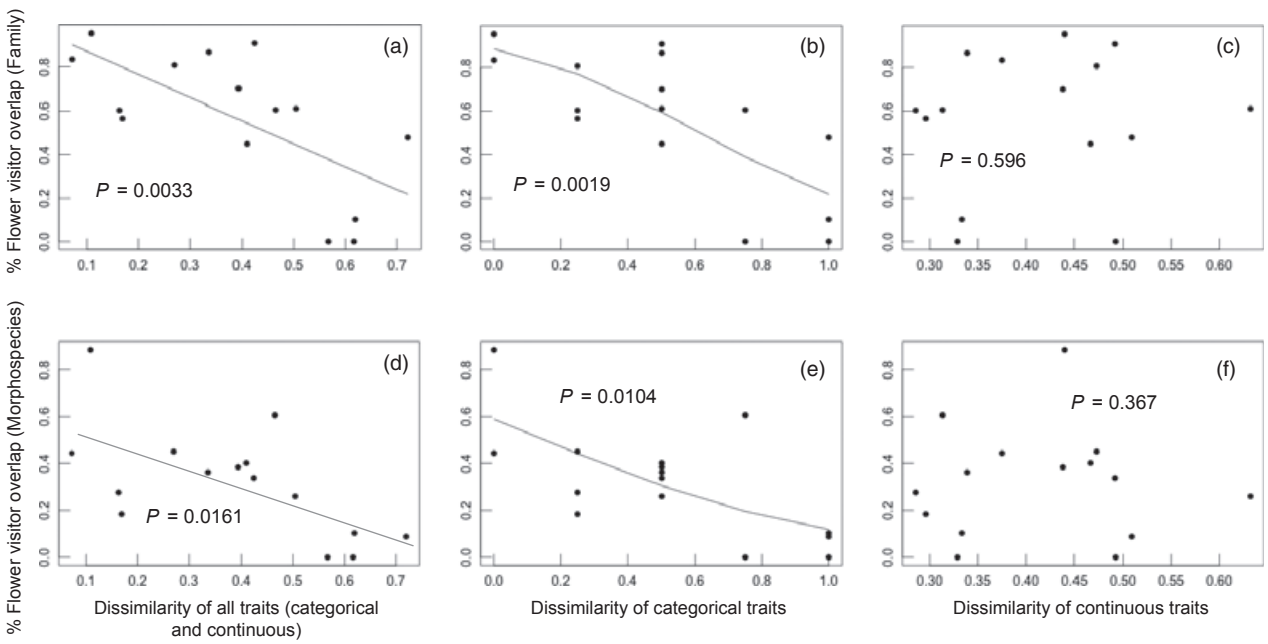

Fig. 2. Results of linear mixed-effects models measuring the response of flower visitor overlap to trait similarity of focal species with *Acacia saligna*. (a–c) show the relationship between flower visitor overlap at the family level and dissimilarity of all, categorical and continuous traits. (d–f) show the relationship between flower visitor overlap at the morphospecies level and dissimilarity of all, categorical and continuous traits. Lines indicate significant relationships. Critical values can be found in Results.

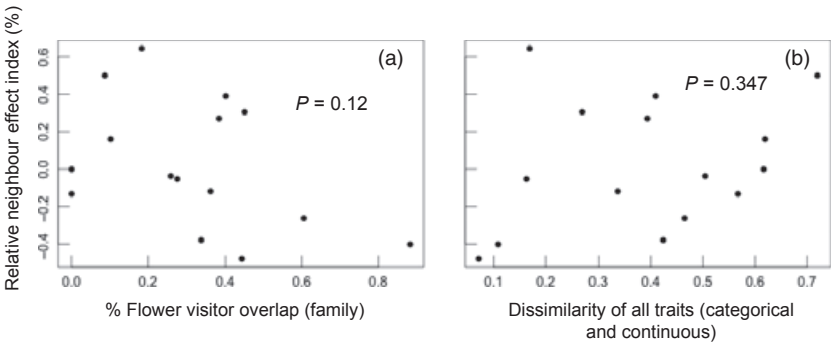

Fig. 3. Results of the linear mixed-effects models measuring the response of relative neighbour effect index to (a) flower visitor overlap at the morphospecies level and (b) trait similarity of focal species with *Acacia saligna*. Lines indicate significant relationships. Critical values can be found in Results.

associated with categorical trait dissimilarity. When testing the relationship between individual categorical traits and flower visitor overlap, we found shape (open; coefficient = 1.70, $t = 2.39$, $P = 0.0330$) to be significant and clustering (solitary; coefficient = −2.22, $t = -2.143$, $P = 0.0516$) to be marginally significant at the morphospecies level. Symmetry (zygomorphic; coefficient = −2.16, $t = -3.494$, $P = 0.00396$) and clustering (solitary; coefficient = −2.08, $t = -2.34$, $P = 0.0359$) were significant at the family level.

Discussion

Similarity in categorical floral traits predicted flower visitor overlap between the invasive *A. saligna* and co-flowering native species. In a related study (Gibson, Pauw and Richardson 2012), we found that the presence of *A. saligna* resulted in significantly reduced visitation to one of the focal species with which it was most florally similar, *Roepera fulva*. Thus, the effect of invasion on different members of the same community depended on their floral traits. This result builds on other studies that found flower clustering, colour, shape and symmetry to be important in predicting how plant species affect each other's pollination (Lázaro, Hegland and Totland 2008; Morales & Traveset 2009; Campbell *et al.* 2010). In our study, the native honeybee (*Apis mellifera* subsp. *capensis*) accounted for the highest proportion of overlap between *A. saligna* and focal species (Table 1). The result is interesting and important because both honeybees and invasive acacias are geographically widespread. Consequently, there is considerable potential for pervasive impacts. This overlap is likely driven by nectar content in the focal species, as nectar is known to be important in the attraction of honeybees.

Overlap of flower visitors of *A. saligna* with thirteen of the focal species in our study indicates *A. saligna* is fairly well integrated into the native visitation network; this supports the findings of previous studies (Memmott & Waser 2002; Lopezaraiza-Mikel *et al.* 2007). There are many possible consequences of flower visitor overlap. Visitor overlap increases the chance of interspecific pollen transfer (Waser 1978). Alien pollen can interfere (mechanically or chemically) with fertilization and may ultimately lead to reduced reproductive success (Brown & Mitchell 2001; but see Tscheulin *et al.* 2009). However, pollinator sharing may not lead to interspecific pollen transfer if the pollinator does not switch between the alien and native plant species (so-called floral constancy) or if foreign pollen is carried on a different body region of the pollinator compared with native pollen (Bartomeus, Bosch and Vilà 2008a; Waterman *et al.* 2011). Australian acacias do not produce floral nectar, so bees are presumably forced to visit surrounding plant species (Bernhardt & Walker 1984).

We found no significant relationship between continuous floral-trait similarity and flower visitor overlap. This is not surprising as the continuous traits in our study quantified differences in total floral display size. While display size is likely to affect visitation rate, it seems less likely that the composition of the visitor fauna should be effected. Furthermore, the considerable variation in display variables seen between the focal species sampled in both years (Table 1) may account for this weak relationship.

Visitation to native species at invaded and uninvaded sites was not significantly influenced by flower visitor overlap or floral-trait similarity (Fig. 3). However, resulting trends are in agreement with higher visitor overlap potentially causing increased competition (i.e. lower RNE value) and increased trait dissimilarity potentially causing less competition (i.e. higher RNE value) between natives and *A. saligna* (Fig. 3). Two features of this particular study system are important to consider regarding the strength of such relationships. Firstly, *Acacia saligna* attracts a wide range of flower visitors. Secondly, the dominant flower visitor of the alien, the honeybee, is often referred to as a 'super generalist' (Olesen, Eskildsen and Venkatasamy 2002). Where relationships are more specialized, stronger effects might be observable. For example, one might expect that the invasive shrub *Nicotiana glauca* will affect the pollination of native plant species with floral features specifically adapted for bird pollination (Geerts & Pauw 2009).

We found a similar response overall of focal species surveyed in 2009 and 2010 to *A. saligna* invasion between years (Appendix S1). In both years, *Chrysanthemoides monilifera* had moderate and low flower visitor overlap with *A. saligna* at the family and morphospecies level, respectively. *Muraltia satureioides* had low visitor overlap with *A. saligna* at the family and morphospecies level, while *Roepera fulva* had high visitor overlap at the family level in both years and high and moderate overlap in 2009 and 2010, respectively, at the morphospecies level. This result increases our confidence in

the ability of floral traits to consistently influence and predict the effect of invasive plants on the native community of plants and pollinators.

Results of logistic regression revealed that categorical floral-trait similarity between *A. saligna* and focal species is driven by similarity in symmetry (actinomorphic) and colour (yellow), while clustering, symmetry and shape similarity were important in driving flower visitor overlap. This is in line with previous studies of honeybee preference that showed traits such as symmetry and colour to be important in flower choice (Neal, Dafni and Giurfa 1998), with a preference for flowers with radial symmetry (Wignall *et al.* 2006).

Our study is a first assessment of the ability of floral-trait similarity to predict the impact of an invasive plant on the pollination of native plants. Future studies could benefit from using pollen deposition and seed production as response variables and including among the predictor variables a measure of spectral reflectance as seen by bees (e.g. ultraviolet reflections; Chittka *et al.* 1994). Invasive plants are becoming permanent members of most native communities. They structure these communities by benefitting some species and suppressing others through direct and indirect interactions. Predicting the outcome remains an important goal.

Acknowledgements

We thank the DST-NRF Centre for Invasion Biology and the Department of Botany and Zoology at Stellenbosch University for funding the research. DMR acknowledges additional funding from the National Research Foundation. Matimba Bolyi, Frank Chidawanyika and Andrew M. Rogers are thanked for assistance in the field. Simon van Noort, Ashley Kirk-Spriggs, Connal Eardley and Şerban Procheş kindly assisted with insect identifications and the Compton Herbarium at Kirstenbosch Gardens helped with plant identifications. We thank Bilton Wine Estate, Donovan Kirkwood, Simon and Shawn Graff, Russell of Walshacres, Mamre Nature Reserve, Sean and Michelle Privett and Steyn Marais of Jakkalsfontein Nature Reserve for permission to work on their land.

References

Alarcón, R. (2009) Congruence between visitation and pollen transport networks in a California plant-pollinator community. *Oikos*, **119**, 35–44.

Bartomeus, I., Bosch, J. & Vilà, M. (2008a) High invasive pollen transfer, yet low deposition on native stigmas in a *Carpobrotus*-invaded community. *Annals of Botany*, **102**, 417–424.

Bartomeus, I., Vila, M. & Santamaria, L. (2008b) Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia*, **155**, 761–770.

Bernhardt, P. & Walker, K. (1984) Bee foraging on three sympatric species of Australian *Acacia*. *International Journal of Entomology*, **26**, 322–330.

Brown, B.J. & Mitchell, R.J. (2001) Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia*, **129**, 43–49.

Campbell, D.R., Bischoff, M., Lord, J.M. & Robertson, A.W. (2010) Flower color influences insect visitation in alpine New Zealand. *Ecology*, **91**, 2638–2649.

Chittka, L., Shmida, A., Troje, N. & Menzel, R. (1994) Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. *Vision Research*, **34**, 1489–1508.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.

Cowling, R.M., Richardson, D.M. & Mustart, P.J. (1997) Fynbos. *Vegetation of Southern Africa* (eds R.M. Cowling, D.M. Richardson & S.M. Pierce), pp. 99–130. Cambridge University Press, Cambridge.

Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd, Chichester, UK.

Danieli-Silva, A., de Souza, J.M.T., Donatti, A.J., Campos, R.P., Vicente-Silva, J., Freitas, L. & Varassin, I.G. (2012) Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high altitude grasslands? *Oikos*, **121**, 35–43.

Dicks, L.V., Corbet, S.A. & Pywell, R.F. (2002) Compartmentalization in plant-insect flower visitor webs. *Journal of Animal Ecology*, **71**, 32–43.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.

Evans, R.D., Rimer, R., Sperry, L. & Belnap, J. (2001) Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications*, **11**, 1301–1310.

Faegri, K. & van der Pijl, L. (1979) *The Principles of Pollination Ecology*. Pergamon Press, Oxford, UK.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. (2004) Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution and Systematics*, **35**, 375–403.

Gallagher, R.V., Leishman, M.R., Miller, J.T., Hui, C., Richardson, D.M., Suda, J. & Trávníček, P. (2011) Invasiveness in introduced Australian acacias: the role of species traits and genome size. *Diversity and Distributions*, **17**, 884–897.

Geerts, S. & Pauw, A. (2009) African sunbirds hover to pollinate an invasive hummingbird-pollinated plant. *Oikos*, **118**, 573–579.

Gibson, M.R., Pauw, A. & Richardson, D.M. (2012) Decreased insect visitation to a native species caused by an invasive tree in the Cape Floristic Region. *Biological Conservation* (in press)

Gibson, M.R., Richardson, D.M., Marchante, E., Marchante, H., Rodger, J.G., Stone, G.N., Byrne, M., Fuentes-Ramírez, A., George, N., Harris, C., Johnson, S.D., Le Roux, J.J., Miller, J.T., Murphy, D.J., Pauw, A., Prescott, M. N., Wandrag, E.M. & Wilson, J.R.U. (2011) Reproductive biology of Australian acacias: important mediator of invasiveness? *Diversity and Distributions*, **17**, 911–933.

Hegland, S.J. & Totland, Ø. (2005) Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecologia*, **145**, 586–594.

Herrera, C.M., Medrano, M., Rey, P.J., Sánchez-Lafuente, A.M., García, M.B., Guitián, J. & Manzaneda, A.J. (2002) Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism- and antagonism-related traits. *Proceedings of the National Academy of Sciences USA*, **99**, 16823–16828.

Higgins, S.I., Richardson, D.M., Cowling, R.M. & Trinder-Smith, T.H. (1999) Predicting the landscape scale distribution of alien plants and their threat to plant diversity. *Conservation Biology*, **13**, 303–313.

Lamarque, L.J., Delzon, S. & Lortie, C.J. (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. *Biological Invasions*, **13**, 1969–1989.

Lázaro, A., Hegland, S.J. & Totland, Ø. (2008) The relationships between floral traits and specificity of pollination systems in three Scandinavian plant communities. *Oecologia*, **157**, 249–257.

Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.-J., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Blignaut, J. & Richardson, D.M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions*, **17**, 1015–1029.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Elsevier Science, Amsterdam, The Netherlands.

Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R. & Memmott, J. (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecology Letters*, **10**, 539–550.

Markham, J.H. & Chanway, C.P. (1996) Measuring plant neighbour effects. *Functional Ecology*, **10**, 548–549.

Memmott, J. & Waser, N.M. (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 2395–2399.

Morales, C.L. & Traveset, A. (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, **12**, 716–728.

Moroń, D., Lenda, M., Skorka, P., Szentgyorgyi, H., Settele, J. & Woyciechowski, M. (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation*, **142**, 1322–1332.

Mucina, L. & Rutherford, M.C. (eds) (2006) *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19*. South African National Biodiversity Institute, Pretoria.

Muñoz, A.A. & Cavieres, L.A. (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *Journal of Ecology*, **96**, 459–467.

Neal, P.R., Dafni, A. & Giurfa, M. (1998) Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypotheses. *Annual Review of Ecology and Systematics*, **29**, 345–373.

Olesen, J.M., Eskildsen, L.I. & Venkatasamy, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions*, **8**, 181–192.

Pauw, A. (2006) Floral syndromes accurately predict pollination by a specialized oil-collecting bee (*Rediviva peringueyi*, Melittidae) in a guild of South African orchids (Coryciinae). *American Journal of Botany*, **93**, 917.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. & R Development Core Team (2011) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1–98.

Pyšek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? *Biological Invasions* (ed W. Nentwig), pp. 97–125. Springer, Berlin.

Pyšek, P. & Richardson, D.M. (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources*, **35**, 25–55.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L. & Rutherford, M.C. (2006) Fynbos biome. *The Vegetation of South Africa, Lesotho and Swaziland* (eds L. Mucina & M.C. Rutherford), pp. 53–219. South African National Biodiversity Institute, Pretoria.

Schlüter, P.M., Ruas, P.M., Kohl, G., Ruas, C.F., Stuessy, T.O.D.F. & Paulus, H.F. (2009) Genetic patterns and pollination in *Ophrys iricolor* and *O. mesaritica* (Orchidaceae): sympatric evolution by pollinator shift. *Botanical Journal of the Linnean Society*, **159**, 583–598.

Stone, G.N., Raine, N.E., Prescott, M. & Willmer, P.G. (2003) Pollination ecology of acacias (Fabaceae, Mimosoideae). *Australian Systematic Botany*, **16**, 103–118.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, **21**, 208–216.

Traveset, A. & Richardson, D.M. (2011) Mutualisms – key drivers of invasions… key casualties of invasions. *Fifty Years of Invasion Ecology. The Legacy of Charles Elton* (ed D.M. Richardson), pp. 143–160. Wiley-Blackwell, Oxford.

Tscheulin, T., Petanidou, T., Potts, S.G. & Settele, J. (2009) The impact of *Solanum elaeagnifolium*, an invasive plant in the Mediterranean, on the flower visitation and seed set of the native co-flowering species *Glaucium flavum*. *Plant Ecology*, **205**, 77–85.

Vogel, S. (1954) Blütenbiologische Typen als Elemente der Sippengliederung: dargestellt anhand der Flora Südafrikas. *Botanische Studien*, **1**, 1–338.

Waser, N.M. (1978) Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia*, **36**, 223–236.

Waterman, R.J., Bidartondo, M.I., Stofberg, J., Combs, J.K., Gebauer, G., Savolainen, V., Barraclough, T.G. & Pauw, A. (2011) The effects of above- and belowground mutualisms on orchid speciation and coexistence. *American Naturalist*, **177**, E54–E68.

Wignall, A.E., Heiling, A.M., Cheng, K. & Herberstein, M.E. (2006) Flower symmetry preferences in honeybees and their crab spider predators. *Ethology*, **112**, 510–518.

Williamson, M. (2001) Can the impacts of invasive species be predicted? *Weed Risk Assessment* (eds R.H. Groves, F.D. Panetta & J.G. Virtue), pp. 20–33. CSIRO Publishing, Collingwood, Vic., Australia.

Received 16 December 2011; accepted 16 April 2012
Handling Editor: Michelle Gibson

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The full set of response and explanatory variables used in final analyses (see Results).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.